The Wilson Journal of Ornithology 119(3):378–385, 2007

PHILOPATRY AND NATAL DISPERSAL OF THE WESTERN SNOWY PLOVER

MARK A. COLWELL,[1,5] SEAN E. McALLISTER,[2] CHERYL B. MILLETT,[1,3] AMBER N. TRANSOU,[2,4] STEPHEN M. MULLIN,[1] ZACH J. NELSON,[1] CAROL A. WILSON,[1] AND RON R. LeVALLEY[2]

ABSTRACT.—Conservation of threatened species requires knowledge of individual movements within and among spatially distinct subpopulations. We quantified philopatry, local dispersal, and number of breeding sites used by 62 Western Snowy Plovers (*Charadrius alexandrinus nivosus*) that were marked as chicks and returned to a breeding area in coastal northern California. Slightly more males (17%) than females (12%) returned to the study area. Natal dispersal (distance between natal nest and first nest as a yearling) was similar for males and females, and greater than reported for other shorebirds. Philopatric plovers dispersed shorter distances between successive nests within a breeding season compared to the distance between successive nests from one year to the next. Most males and females that bred locally wintered in the study area. Those that wintered locally tended to be from later clutches compared to the few migrants that hatched earlier in the season. The population of Snowy Plovers in coastal northern California is linked by dispersal with other breeding plovers along the Pacific coast. Dispersal estimates indicate that wide-ranging movements are typical of Snowy Plovers throughout their range, which should facilitate recolonization of habitats. *Received 17 March 2006. Accepted 4 September 2006.*

Conservation efforts for rare and patchily distributed species require knowledge of patterns and causes of dispersal of individuals among and within subpopulations. These data help biologists understand the genetic structure of populations (Avise and Hamrick 1996) and may enhance efforts to manage reproductive success. Dispersal estimates, as well as demographic data on survival and reproduction, are key elements of models predicting population persistence and recovery (Morris and Doak 2002). Dispersal is quantified in one of two ways (Oring and Lank 1984). First, philopatry is often gauged by the proportion of birds of either gender returning to breed at a location, although "return" at times is defined as an individual being observed (Colwell et al. 1988, Reynolds and Cooke 1988). This definition fails to distinguish between individuals seen once versus multiple times (resident) in an area. In contrast, natal dispersal quantifies the distance moved by a philopatric individual from its natal site to where it first breeds.

The Snowy Plover (*Charadrius alexandrinus*) in North America is divided into two subspecies (Page et al. 1995, Funk et al. 2007). One (*C. a. tenuirostris*) breeds in the Caribbean and a second (*C. a. nivosus*) is distributed in the western Great Plains, Great Basin, and along the Pacific coast. The U.S. Fish and Wildlife Service listed the Pacific coastal population segment in 1993 as threatened under the Endangered Species Act (U.S. Department of Interior 1993). The listed population segment has been well studied for over a quarter century (e.g., Warriner et al. 1986, Page et al. 1991). Stenzel et al. (1994, 2007) documented dispersal of a population in central California. Males and females occasionally dispersed long distances (50–1,140 km) within and between breeding seasons, and females were more likely than males to be absent from their primary site during a portion of the breeding season. Stenzel et al. (1994) interpreted these patterns as a consequence of the species' long breeding season (~120 days of egg laying), uniparental (male) care of chicks, and dynamic breeding habitats. These features allow females to nest successfully up to three times, often at widely disjunct locations.

The recovery plan for the listed population segment of the Western Snowy Plover (U.S.

[1] Department of Wildlife, Humboldt State University, Arcata, CA 95521, USA.

[2] Mad River Biologists, 920 Samoa Blvd., Ste 210, Arcata, CA 95521, USA.

[3] The Nature Conservancy, Lake Wales Ridge Program, P. O. Box 630, Babson Park, FL 33827, USA.

[4] California State Parks, P. O. Box 2006, Eureka, CA 95502, USA.

[5] Corresponding author; e-mail: mac3@humboldt.edu

Department of Interior 2001) designated six recovery units extending from the northern limit of the species' breeding range in Washington south through California. Most breeding plovers in coastal northern California (Recovery Unit 2) are concentrated at a few locations around Humboldt Bay (Colwell et al. 2005b), which are several hundred km from other large concentrations of breeding plovers north and south. Recovery Unit 2 is targeted for a population of 150 breeding plovers (U.S. Department of Interior 2001), but the population has not reached this level, varying between 54 and 74 adults over a 6-year period (2001–2006; Mullin 2006).

We initiated a study in 2000 to individually mark breeding plovers in Recovery Unit 2. Our objectives were to examine gender differences in (1) return of plovers marked as chicks to the local breeding population, and (2) dispersal from natal nest to first and subsequent nests.

STUDY AREA

We studied plovers from 2000 to 2006 in Del Norte, Humboldt, and Mendocino counties in northern California (Fig. 1). We conducted most fieldwork in Humboldt County where the majority of plovers bred, but observers from state and federal agencies conducted bimonthly surveys of suitable breeding habitat throughout Recovery Unit 2. Plovers bred in two distinct habitats in the study area (Colwell et al. 2005b). Many plovers nested in fine, sandy substrates of ocean-fronting beaches amidst sparse debris fields of dried brown algae, shells, dead vegetation, driftwood, and occasional garbage. These beaches were often vegetated sparsely with native plants (e.g., *Abronia*, *Leymus*), dense stands of introduced European dune grass (*Ammophila arenaria*), and patches of sea rocket (*Cakile*). Plovers also nested on gravel bars of the lower Eel River near its confluence with the Pacific Ocean upriver approximately 16 km (Colwell et al. 2005b). Plovers breeding along the river nested in coarse, heterogeneous substrates varying in size from sand to pea-sized gravel and large stones, which were vegetated sparsely by willow (*Salix* spp.) and white sweet clover (*Melilotus alba*).

METHODS

We began marking adult plovers and newly hatched chicks in 2000, 1 year prior to initiating an intensive monitoring program. Each year, we captured breeding adults at nests using noose mats and circular walk-in nest traps. We marked adults with a unique combination of a federal aluminum band (wrapped in colored tape) and three colored leg bands. We marked all siblings of a brood at hatch with an aluminum band wrapped with brood-specific colored tape, which allowed us to distinguish between similar-age chicks from different broods in an area. We are confident that we captured and banded >95% of all newly hatched chicks and breeding adults in the study area each year. We recaptured adults that we first marked as chicks and marked them with unique adult band combinations. Observers surveyed breeding plovers almost daily in each habitat from mid March to early September. We recorded the identity of banded plovers, found nests, and monitored broods during surveys. Upon finding a nest, we recorded the number of eggs and estimated hatch date (for complete clutches) using egg flotation methods (Alberico 1995). We estimated hatch date for incomplete clutches by adding 27 days (average incubation period; Page et al. 1995) to the date the last egg was laid. We erected predator exclosures at most (61%) nests on beaches but did not construct exclosures around nests along rivers. We monitored fledging success of plovers beginning in 2001 through 2006 (Colwell et al. 2005a, 2007) by visiting sites with broods at 1–4 day intervals and recording the presence of adults and young until chicks fledged at 28 days (Page et al. 1995).

We defined philopatry as the breeding of a locally-hatched chick in the study area (coastal northern California; Recovery Unit 2 [RU2]) or repeated sightings during the nesting season suggesting breeding or attempted breeding. We quantified natal dispersal as the straight-line distance (m) between an individual's natal nest and its first nest as a yearling using a geographic information system. We categorized breeding dispersal, the distance between successive nests of an individual in two ways. Within-season dispersal was the distance between successive nests in a given

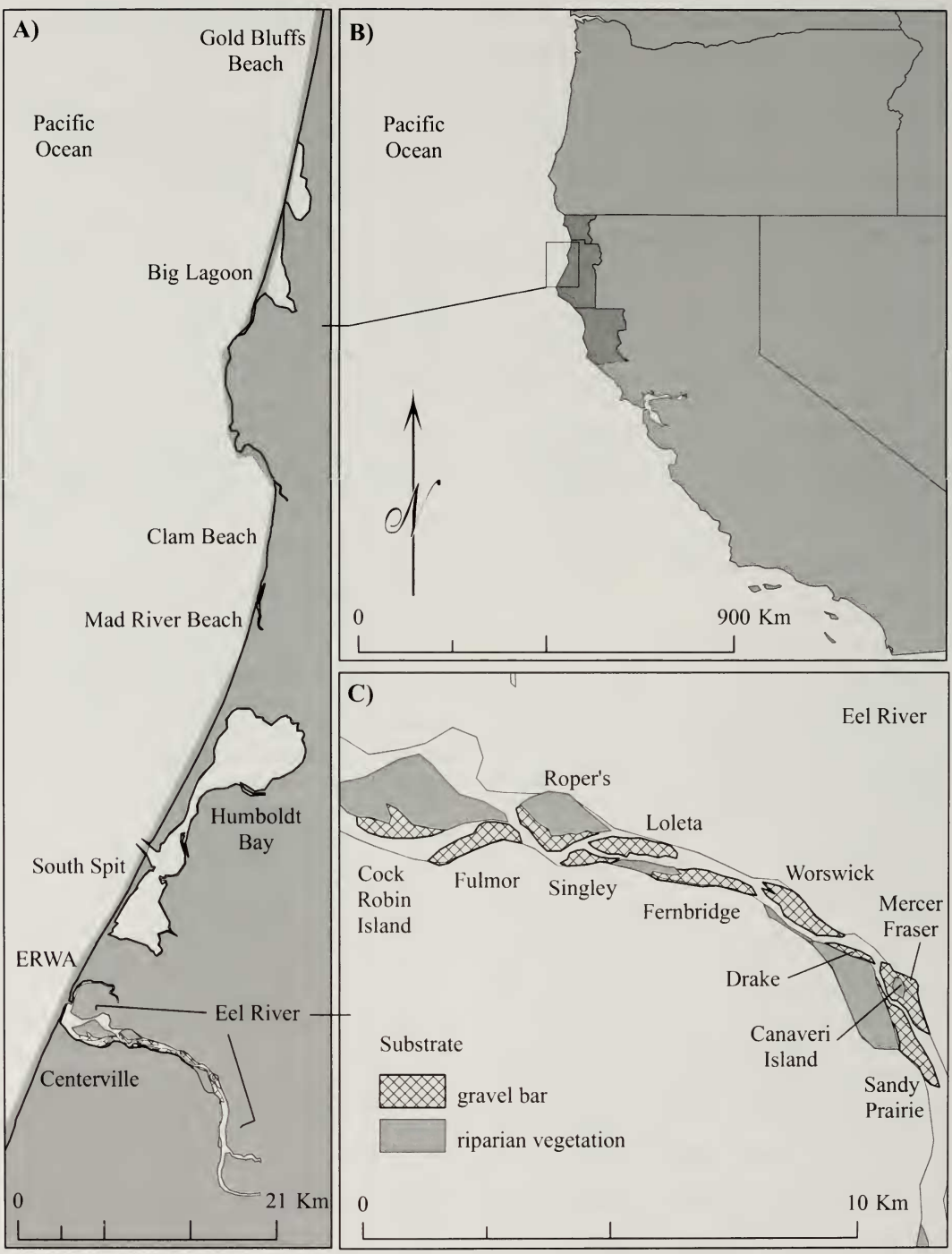

FIG. 1. Study areas (A) in the three counties of coastal northern California that comprise Recovery Unit 2; (B) where Snowy Plovers were color-marked and monitored from 2000 to 2006. Individual gravel bars along the lower Eel River are shown in (C).

TABLE 1. Philopatry of Snowy Plovers breeding in coastal northern California, 2001–2006.

Year	Total # banded previous year	% Return Females (n)[a]	% Return Males (n)[a]
2006	71	11 (4)	17 (6)
2005	76	11 (4)	16 (6)
2004	61	13 (4)	13 (6)
2003	69	14 (5)	12 (4)
2002	93	13 (6)	17 (8)
2001	58	7 (2)	24 (7)
Totals	428	11.7 (25)	17.3 (37)

[a] Assumes an equal sex ratio among newly hatched chicks (Székely et al. 2004).

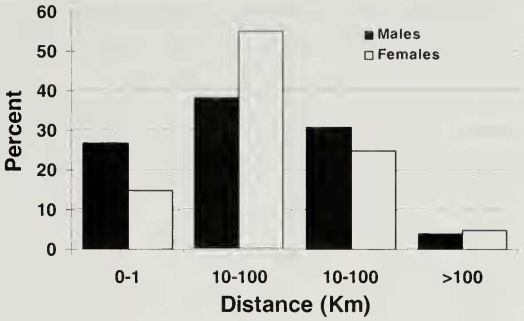

FIG. 2. Dispersal distances of Snowy Plovers (females [□, n = 20] and males [■, n = 26]) in coastal northern California.

breeding season; between-year dispersal was the distance between an individual's first nest of the year and the location of its last nest of the previous year. We summarized data for males and females separately, and distinguished between nests in which eggs failed to hatch and those in which at least one egg successfully hatched. We tallied the number of breeding locations occupied by individuals based on observations of color-marked birds. We defined a location (e.g., gravel bar or linear stretch of beach) as a breeding site occupied by one or more plovers, often separated by unsuitable (e.g., river channel, rocky intertidal) or unoccupied (e.g., long stretches of beach) habitat from other locations by a distance greater than the extent of any particular site (Fig. 1). We collated data over weekly intervals spanning 15 March to 15 July, the period in which plovers initiated nests (Colwell et al. 2005b) and prior to the formation of post-breeding flocks.

We analyzed return rates using Chi-square tests, assuming an equal sex ratio at hatch (Székely et al. 2004). Each individual plover was considered once in this analysis (i.e., returned either as a yearling or 2 years of age). We summarized dispersal as $\bar{x} \pm$ SD, and compared samples for males and females using a t-test of untransformed linear distances between an individual's natal nest and first known nest as an adult. We used logistic regression to examine relationships between date of hatching for an individual and whether or not it was observed as a winter resident or migrant. We used SAS (SAS Institute 1991) to analyze data.

RESULTS

Philopatry and Natal Dispersal.—Sixty-two (14.4%) of 432 marked chicks returned to the study area; most (94%) bred locally as yearlings (Table 1). Four of the 62 philopatric plovers (6.5%) were observed repeatedly during a breeding season suggesting they nested locally; however, we did not find nests for these individuals. Philopatry (of males and females combined) annually ranged from 13.0 to 16.4%. Males (17.3%) tended to be more philopatric than females (11.7%) (X^2 = 2.72, df = 1, P = 0.10). There was no gender difference in natal dispersal ($t_{26,20}$ = 0.23, P = 0.82) (Fig. 2). Female and male yearlings established first nests within northern California (RU2) at distances of 16.0 ± 29.2 km (median = 4.8, range = 0.4–125.7) and 18.2 ± 33.6 km (median = 5.0, range = 0.06–163.8), respectively, from their natal nests. Considering only the years 2001 through 2005 when we intensively monitored fledging success, 53 (31.5%) of 168 fledged chicks returned to the northern California study area.

Philopatric plovers comprised 10–22% of the local breeding population each year. Plovers bearing bands from Recovery Unit 2 have been recaptured or observed during the breeding season elsewhere along the Pacific coast (Table 2). A yearling female dispersed 474 km from the local population in 2005 to breed at Moss Landing, California after high water on the Eel River destroyed her initial nest. Another female, hatched in 2000, dispersed 354 km to breed in Oregon; she subsequently returned to breed in Humboldt

TABLE 2. Snowy Plover dispersal to breed outside of coastal northern California.

Hatch year	Gender	Breeding location	Year bred
1999	F	Siltcoos, OR	
2000	M	New River, OR	2003
2000	F	Tahkenitch, OR	2001
2000	F	Bandon, OR	2001
2001	M	Sutton Beach and Coos Bay, OR	2002–04
2001	F	New River and Bandon, OR	2003, 2005
Unknown	M	Sutton Beach, OR	2001
Unknown	M	Leadbetter Pt. and Willapa Bay, WA	2002
Unknown	M	Midway Beach, WA	2002
Unknown	F	Bandon, OR	2002
Unknown	Unk	Pt. Reyes, CA	2002
Unknown	M	Pt. Reyes, CA	2003
Unknown	Unk	Vandenberg, CA	2003
2004	F	Moss Landing, CA	2005
2004	F	Leadbetter Pt., WA	2005
2004	M	Leadbetter Pt., WA	2005
2004	M	Leadbetter Pt., WA	2005

County (2003) and Mendocino County (2004).

A greater percentage of river-hatched plovers returned to the study area (16.3% of 203 chicks) compared to beaches (7.9% of 229 hatched chicks). However, this analysis was based on chicks marked at hatch. Return rates based on fledged chicks were similar (31.0% of 58 chicks fledged from beaches; 30.0% of 110 river-fledged chicks). Most (69.4% of 49) philopatric plovers first bred in their natal habitats (i.e., beach vs. river); 30.6% (15 of 49 yearlings) switched habitats. Similar numbers of yearling males and females (n = 16 total birds) moved from their natal beach habitat to breed on the river (four males and three females), and from natal river habitat to breed on the beach (three males and five females). Two plovers (one male and one female) were absent as yearlings but returned to breed when they were 2 years of age in their natal river habitat; one male plover first bred on his natal beach as a 2-year-old.

Between-year and Within-season Dispersal.—Individuals typically moved greater distances between than within years (Table 3). There was no clear difference in the average distance moved by either males or females that were successful or failed to hatch their first clutch. There was no difference (Mann-Whitney U-test, z = 0.83, P = 0.43) in dispersal distance between two successful (10.7 ± 14.3 km) and six unsuccessful (2.3 ± 2.8 km) males or between five successful (0.4 ± 0.4 km) and four unsuccessful (118.7 ± 236.8 km) females (Mann-Whitney U-test, z = 0.37, P = 0.71).

Within a year, individuals commonly bred at a single site (yearlings and older adults combined; males: 86–100% and females: 76–90%) within the study area, rather than moving among sites (Fig. 1). This pattern was higher (4–14% annually) for males than females in each year. As yearlings, males (1.9 ± 1.0) and females (1.6 ± 0.9) bred at similar numbers of sites, and the number of breeding sites was similar as individuals bred in their second (males: 1.9 ± 1.1; females: 1.9 ± 1.2), third (males: 1.6 ± 1.2; females: 1.7 ± 1.0) or fourth year (males: 1.0 ± 0.0; females: 1.5 ± 0.7).

Migratory Movements and Winter Residency.—Most philopatric plovers were resident year-round, as evidenced by repeated observations in post-breeding and winter flocks. Fourteen of 17 philopatric males observed during winter occurred at one of several sites where flocks form near breeding areas (Clam Beach, South Spit, and at the mouth of the Eel River). Three other philopatric males wintered in southern California. Nine of 11 philopatric females (with known wintering sites) wintered locally; two wintered south of the study area. There was a tendency for individuals (males and females combined, n = 27) that hatched from early clutches to become migrants

TABLE 3. Distance (km) ($\bar{x} \pm$ SD) between successive nests of male and female Snowy Plovers.

Age	Nesting attempt	Females		Males	
		Fate of previous nest		Fate of previous nest	
		Hatched (*n*)	Failed (*n*)	Hatched (*n*)	Failed (*n*)
Yearling	2nd	0.4 ± 0.4 (5)	118.7 ± 236.8 (4)	10.7 ± 14.3 (2)	2.3 ± 2.8 (6)
	3rd				0.9 ± 1.1 (4)
	4th				0.7 ± 0.8 (2)
Second Yr	1st	10.4 ± 20.4 (5)	15.4 ± 24.3 (3)	11.7 ± 20.2 (12)	1.9 ± 2.4 (5)
	2nd	2.2 ± 2.5 (2)	1.2 ± 1.5 (3)	1.0 ± 0.8 (3)	1.5 ± 1.2 (8)
	3rd		2.7 ± 2.3 (5)	0.7 ± 0.4 (4)	1.7 ± 1.9 (2)
	4th		0.9 ± 0.2 (2)		0.9 ± 0.6 (4)
	5th		23.5 ± 31.8 (2)		47.5 ± 0.0 (1)
Third Yr	1st	9.0 ± 15.8 (6)	0.2 ± 0.0 (1)	2.9 ± 4.3 (8)	2.0 ± 2.3 (2)
	2nd		2.1 ± 2.0 (5)	0.5 ± 0.6 (3)	0.8 ± 1.1 (4)
	3rd	2.8 ± 0.0 (1)	0.1 ± 0.0 (1)		1.3 ± 1.0 (3)
	4th				0.7 ± 0.6 (2)
	5th				0.6 ± 0.6 (2)
	6th				0.1 ± 0.0 (1)
Fourth Yr	1st		6.1 ± 0.0 (1)	21.2 ± 36.4 (3)	4.9 ± 0.0 (1)
	2nd				0.9 ± 0.4 (2)
	3rd				1.1 ± 0.0 (1)
	4th				2.7 ± 0.0 (1)
	5th				1.3 ± 0.0 (1)
Fifth Yr	1st			3.2 ± 0.0 (1)	

whereas individuals from later clutches were more likely to become local winter residents ($\beta = 0.05 \pm 0.03$, Wald $X^2 = 3.25$, $P = 0.07$).

DISCUSSION

Male and female Snowy Plovers in coastal northern California had similar patterns of natal dispersal and use of breeding sites; males tended to be more philopatric than females. These findings are similar to patterns from a long-term study (with a much larger sample) in central California (Stenzel et al. 2007). In the Monterey Bay area, philopatry was male biased, a pattern reported for most other shorebirds where gender differences exist. Oring and Lank (1984) concluded there was a tendency for male-biased philopatry among the 12 species of shorebirds they reviewed. Recent studies strengthen the case for male-biased philopatry. Jackson (1994) reported that males and females of three territorial shorebirds (Redshank [*Tringa totanus*], Dunlin [*Calidris alpina schinzii*], and Ringed Plover [*Charadrius hiaticula*]) breeding in the Western Isles, United Kingdom returned at similar rates and that males settled significantly nearer their natal sites than females. Pierce (1989) reported a similar finding of male settlement nearer natal sites for the Banded Dotterel (*Charadrius bicinctus*) in New Zealand. Gratto (1988) reported no gender bias in philopatry for the Semipalmated Sandpiper (*Calidris pusilla*).

The Snowy Plover has a serially polygamous, territorial mating system; males and females share incubation, but males typically care for chicks alone while females pursue additional mates (Page et al. 1995). As a consequence, during the long (~120 day) breeding season typical of the species along the Pacific coast, females may breed successfully up to three times whereas males may breed twice. The Snowy Plover occupies dynamic habitats that vary greatly in quality owing to frequent natural disturbance (e.g., tidal over-wash, river flooding, drifting sand). Coupled with high nest failure rates from predation (Page et al. 1995; Colwell et al. 2005a, 2005b), these facets place a premium on dispersal rather than being faithful to a particular nest site (Stenzel et al. 1994). We found no relationship between nesting success and breeding dispersal; a finding also reported by Stenzel et al. (1994), but in contrast to other shorebirds (Oring and Lank 1984).

Comparatively large dispersal distances of

Snowy Plovers in this study were similar to those reported by Stenzel et al. (1994, 2007) for Snowy Plovers of varying age. For both populations, the comparatively large dispersal distances may stem from two facets related to the spatial scale of study, the first methodological and the second biogeographical. First, we intensively monitored dispersal over a large area. Jackson (1994) quantified dispersal by intensively monitoring shorebirds on four study plots of 40–120 ha separated by a few km of suitable habitat, which he surveyed occasionally for dispersing birds. Jackson's (1994) study areas roughly correspond in size to each of our locations. Dispersal estimates for Snowy Plovers would have been comparable to those for Ringed Plover (1.5 and 2.4 km for males and females, respectively) had we limited the spatial scale of our study area to similar sized plots. Second, the disjunct distribution of breeding sites may have also contributed to large average dispersal distances. Average dispersal distance for both males and females approached 20 km (median distances were ~5 km and comparable to those reported by Stenzel et al. 2007). The average dispersal distance is intermediate between movements within and between locations (e.g., Clam Beach, South Spit, and gravel bars of the Eel River). Our dispersal estimates combine two groups of plovers: (1) those that would be considered truly philopatric as they returned to within a few km of their natal site, and (2) those that remained in the local area but moved in excess of 10 km to breed first at a location other than their natal site.

The breeding population of Snowy Plover in coastal northern California consists of a mix of year-round residents and migrants similar to that reported for central California (Stenzel et al. 1994). The tendency to become migratory versus resident correlated with timing of an individual's fledging in the population; chicks from late hatching clutches were more likely to become residents. Pierce (1989) reported similar findings for the Banded Dotterel. We offer the following scenario for the development of resident versus migrant behaviors in Snowy Plovers. The tendency for plovers from early and late hatching clutches to become migratory and resident, respectively, may stem from the proximity of a post-breeding flock for a juvenile to join. Specifically, chicks from early hatching clutches may become migrants because they develop a tendency to wander in search of other plovers when most adults are still breeding. In contrast, late-hatching chicks often fledge in the vicinity of post-breeding flocks, which begin to form in mid-July in our study area and elsewhere (Stenzel et al. 1994). Thus, we speculate that late season young are incorporated into what will become the wintering flock and establish their winter residency patterns. If this scenario is accurate, it may explain the increasing evidence that habitat protection for non-breeding flocks can lead to establishment of breeding plovers at wintering sites (Lafferty 2001).

CONSERVATION IMPLICATIONS

Breeding Snowy Plovers in coastal northern California are linked through dispersal with subpopulations elsewhere in the range of the listed population segment. Large dispersal distances of yearlings may be a consequence of this isolation and disjunct breeding locations. Individuals occasionally move long distances (to breed) both north and south on the Pacific coast (Stenzel et al. 1994, 2007). These large movements indicate that plovers are capable of colonizing suitable habitat throughout the species' range. The establishment of local breeders, however, may be enhanced by the presence of flocks of post-breeding plovers when fledglings search for a wintering site. The absence of a relationship between nesting success and dispersal strengthens findings of Stenzel et al. (1994) who suggested that wide-ranging movements of individuals were a consequence of the species' long breeding season, sequentially polygamous mating system, use of dynamic breeding habitats, and frequent nest failure. Individuals move widely among multiple sites within and among breeding seasons to capitalize on breeding habitat of varying quality, including the availability of mates (Stenzel et al. 1994). Wide-ranging movements suggest that plovers are capable of colonizing formerly unoccupied sites such as newly restored habitats and those areas afforded enhanced protection under the Endangered Species Act.

ACKNOWLEDGMENTS

B. P. Atkinson, H. E. Beeler, N. S. Burrell, A. M. Clarke, T. J. L. Colwell, W. P. Goldenberg, M. A. Har-

dy, S. J. Hurley, T. L. Klemetson, A. J. Leist, D. M. LeValley, J. J. Meyer, G. B. Reid, K. G. Ross, and R. R. Smith assisted in the field on many occasions; numerous volunteers and individuals from state and federal agencies conducted surveys in Del Norte, Humboldt, and Mendocino counties. We are grateful to Jim Watkins for supporting our efforts. Comments of several anonymous reviewers and G. W. Page improved the manuscript. Our work was funded by the California Department of Fish and Game, California Department of Parks and Recreation, Humboldt County Fish and Game Advisory Commission, Humboldt County Planning Department, Humboldt State University, Mad River Biologists, Marin Rod and Gun Club, MRB Research, Inc., Redwood Region Audubon Society, Stockton Sportsmen's Club, Western Section of The Wildlife Society, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, and the California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis.

LITERATURE CITED

Alberico, J. A. R. 1995. Floating eggs to estimate incubation stage does not affect hatchability. Wildlife Society Bulletin 23:212–216.

Avise, J. C. and J. L. Hamrick (Editors). 1996. Conservation genetics. Chapman and Hall, New York, USA.

Colwell, M. A., S. J. Hurley, J. N. Hall, and S. J. Dinsmore. 2007. Age-related survival and behavior of Snowy Plover chicks. Condor 109:638–647.

Colwell, M. A., J. D. Reynolds, C. L. Gratto, D. Schamel, and D. M. Tracy. 1988. Phalarope philopatry. Congressus Internationalis Ornithologici 19:585–593.

Colwell, M. A., Z. Nelson, S. Mullin, C. Wilson, S. E. McAllister, K. G. Ross, and R. LeValley. 2005a. Final report: 2005 Snowy Plover breeding in coastal northern California, Recovery Unit 2. Submitted to MRB Research, Inc., Arcata, California, USA.

Colwell, M. A., C. B. Millett, J. J. Meyer, J. N. Hall, S. J. Hurley, S. E. McAllister, A. N. Transou, and R. R. LeValley. 2005b. Snowy Plover reproductive success in beach and river habitats. Journal of Field Ornithology 76:373–382.

Funk, W. C., T. D. Mullins, and S. M. Haig. 2007. Conservation genetics of Snowy Plovers (*Charadrius alexandrinus*) in the Western Hemisphere: population genetic structure and delineation of subspecies. Conservation Genetics: In press.

Gratto, C. L. 1988. Natal philopatry, site tenacity, and age of first breeding of the Semipalmated Sandpiper. Wilson Bulletin 100:660–663.

Jackson, D. B. 1994. Breeding dispersal and site-fidelity in three monogamous wader species in the Western Isles, U.K. Ibis 136:463–473.

Lafferty, K. D. 2001. Human disturbance to wintering Snowy Plovers at a southern California beach. Biological Conservation 10:1–14.

Morris, W. F. and D. F. Doak. 2002. Quantitative conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Mullin, S. M. 2006. Apparent survival and population growth of Western Snowy Plovers (*Charadrius alexandrinus nivosus*) in Humboldt County, California. Thesis. Humboldt State University, Arcata, California, USA.

Oring, L. W. and D. B. Lank. 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. Pages 125–147 *in* Shorebirds: breeding behavior and populations (J. Burger and B. L. Olla, Editors). Plenum Press, New York, USA.

Page, G. W., L. E. Stenzel, D. W. Shuford, and C. R. Bruce. 1991. Distribution and abundance of the Snowy Plover on its western North American breeding grounds. Journal of Field Ornithology 62:245–255.

Page, G. W., J. S. Warriner, J. C. Warriner, and P. W. C. Paton. 1995. Snowy Plover (*Charadrius alexandrinus*). The birds of North America. Number 154.

Pierce, R. J. 1989. Breeding and social patterns of Banded Dotterels (*Charadrius bicinctus*) at Cass River. Notornis 36:13–23.

Reynolds, J. D. and F. Cooke. 1988. The influence of mating systems on philopatry: a test with the polyandrous Red-necked Phalarope. Animal Behavior 36:1788–1795.

SAS Institute, Inc. 1991. SAS System for regression. Second Edition. SAS Institute Inc., Cary, North Carolina, USA.

Stenzel, L. E., J. C. Warriner, J. S. Warriner, K. S. Wilson, F. C. Bidstrup, and G. W. Page. 1994. Long-distance breeding dispersal of Snowy Plovers in western North America. Journal of Animal Ecology 63:887–902.

Stenzel, L. E., G. W. Page, J. C. Warriner, J. S. Warriner, D. E. George, C. R. Eyster, B. A. Ramer, and K. K. Neuman. 2007. Survival and natal dispersal of juvenile Snowy Plovers in central coastal California. Auk 124: In press.

Székely, T., I. C. Cuthill, S. Yezerinac, R. Griffiths, and J. Kis. 2004. Brood sex ratio in the Kentish Plover. Behavioral Ecology 15:58–62.

U.S. Department of Interior. 1993. Threatened status for the Pacific coast population of the Western Snowy Plover. Federal Register 58:12864–12874.

U.S. Department of Interior. 2001. Western Snowy Plover (*Charadrius alexandrinus nivosus*). Pacific coast population draft recovery plan. Portland, Oregon, USA.

Warriner, J. S., J. C. Warriner, G. W. Page, and L. E. Stenzel. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. Wilson Bulletin 98:15–37.